Stomatal and Nonstomatal Regulation of Water Use in Cotton, Corn, and Sorghum[1]

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ABSTRACT

Stomata of corn (*Zea mays* L.) and sorghum (*Sorghum bicolor* L.) responded to changes in leaf water potential during the vegetative growth phase. During reproductive growth, leaf resistances were minimal and stomata were no longer sensitive to bulk leaf water status even when leaf water potentials approached −27 bars. Stomata of corn, cotton (*Gossypium hirsutum* L.), and sorghum appear to respond to changes in the humidity deficit between the leaf and air and in this manner, regulated transpirational flux to some degree. Distinct differences in water transport efficiency were observed in the three species. Under nonlimiting soil water conditions, sorghum exhibited the greatest efficiency of water transport while under limiting soil moisture conditions, cotton appeared most efficient. Corn was the least efficient with respect to nonstomatal regulation of water use. Differences in drought tolerance among the three species are partially dependent on stomatal regulation of water loss, but efficiency of the water transport system may be more related to drought adaptation. This is particularly important since stomata of all three species did not respond to bulk leaf water status during a large portion of the growing season.

The responses of stomata to leaf water status and environment are important in regulating transpiration and photosynthesis. The relationships between stomatal resistance, leaf water potential, leaf temperature, and environmental factors such as temperature and humidity are particularly important to plants growing in arid or semiarid conditions. Stomatal regulation, or adjustments that facilitate CO_2 diffusion while minimizing water loss, might enhance the drought tolerance of plants subjected to temporal or sustained water deficits.

Numerous studies have revealed that increased leaf diffusive resistance results from progressive depressions of leaf water potentials (4, 8, 9, 13, 24, 25). The sensitivity of stomata to water deficits decreases with increasing leaf age in cotton (23) and, in the case of cotton and sorghum, stomata tend to be less responsive to water stress if the plants have been previously subjected to mild water deficits (6, 18). Stomata of field-grown plants often respond to leaf water potential in an entirely different manner when compared with similar plants established in growth chambers (1, 14, 25).

Stomatal response to humidity, independent of bulk leaf

water status, has been suggested as a mechanism of enhancing water use efficiency (10, 12, 17, 21). Increased humidity gradients between leaf and ambient air increased leaf resistance in citrus (10), sunflower and bean (11), sesame (12), Engelman spruce (16), and various desert species (17, 21). Although some of these investigations were of a laboratory nature (10–12), field studies reflect the importance of this mechanism in maximizing water use efficiency (16, 17, 21).

These experiments were conducted to ascertain the responses of stomata of field-grown plants to leaf water status and humidity, changes in stomatal response characteristics during plant development, and the nonstomatal regulation of water use.

MATERIALS AND METHODS

Experiments were conducted on field-grown sorghum (*Sorghum bicolor* L. Moench cv. Pioneer 42004 and 22516), corn (*Zea mays* L. cv. DeKalb XL63 and XL75), and cotton (*Gossypium hirsutum* L. cv. Coker 5110 and SP37). The specific genotypes utilized in this study represented different growth habits or morphological differences: a senescent (22516) and nonsenescent (42004) sorghum; medium (XL63) and late (XL75) maturing corn; and determinate (SP37) and indeterminate (5110) cotton. Genotypes of contrasting growth habits were used to ascertain the existence of any genotypic differences in the regulation of water use. However, no genotypic differences were observed and the data were pooled and reported on a species basis. Detailed specifications of the field plots can be found in Ackerson et al. (2). Preliminary investigations were made in 1975 (1, 2) and further experiments were conducted during 1976. The data obtained during June, July, and August 1976 are reported in the present study. For the 1976 studies, sorghum and corn were planted on May 10 and cotton on June 4. Visible evidence of reproductive growth was observed in corn on June 20, in sorghum on June 27, and first bloom in cotton on August 4.

Differential levels of irrigation were established based on minimum daily leaf water potentials. Irrigation of plants when leaf water potentials declined to −17 bars is defined as nonlimiting soil water conditions, whereas irrigation at −27 bars indicates limiting soil water conditions. Nonlimiting soil water conditions refer to a soil profile (top 60 cm) with less than 40% of the available water having been depleted. A limiting soil water condition represents a similar profile in which the available water has been depleted in excess of 60%. This particular soil holds approximately 12 cm of available water in the top 60 cm. Measurements of soil water status were conducted with a neutron probe and representative values of soil water potential have been described (2). Measurements of leaf water potential, stomatal resistance, leaf and air temperatures and humidity were obtained several times during the day (beginning ∼ 0900 CDT) and on numerous days during the course of the growing

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season. Instrumentation for data collection included a pressure chamber (leaf water potential), diffusion porometer calibrated according to Kanemasu et al. (15) to obtain stomatal resistance, wet and dry bulb psychrometer (air temperature and humidity), and a WAHL IR thermometer (leaf temperature). Pressure chamber values were obtained from leaf blade tissue of sorghum and corn and petioles of cotton. We have made comparisons of xylem pressure potential using the pressure chamber and leaf water potential utilizing leaf discs in a thermocouple psychrometer. Reasonable agreement (± 1.0 bar) was found between the two methods above −22 bars leaf water potential, but larger differences were evident when leaf water potentials were less than −22 bars. Within the range of potentials normally observed during this study (−10 to −25 bars), the pressure chamber gave reasonable estimates of plant water status.

Diffusive resistances were obtained on both shaded and nonshaded leaves. However, in order to derive the various relationships between stomatal resistance and other parameters, only data obtained at light intensities sufficient to saturate the stomatal opening response were utilized in this study (> 1500 $\mu E \cdot m^{-2} \cdot sec^{-1}$ photosynthetically active radiation). Abaxial and adaxial stomatal resistances were obtained in order to obtain total leaf resistance, calculated by assuming individual surface resistances acted in parallel. Transpiration was calculated by determining absolute humidity differences between leaf and air and dividing by the sum of the leaf and boundary layer resistances. Boundary layer resistances were estimated using moist filter paper and ranged from 0.2 to 0.5 sec cm^{-1} (10). Transpiration rates were determined after initiation of reproductive growth in corn and sorghum and throughout the growing season in cotton.

During vegetative growth, data were collected on the youngest collared leaf of corn and sorghum. Subsequently, data were obtained on the uppermost fully expanded leaves of cotton and the flag and first leaf immediately below the flag leaf of sorghum and corn. Throughout the course of the study, flag and first leaves of both corn and sorghum responded similarly with respect to regulation of water use.

RESULTS AND DISCUSSION

Stomatal regulation of water loss, as reflected by increasing leaf resistances in response to decreasing leaf water potentials, was evident in both corn and sorghum during the vegetative growth phase of both species (Fig. 1). The data support observations by Sanchez-Diaz and Kramer (20) indicating similar values of leaf resistance at equivalent leaf water potentials in
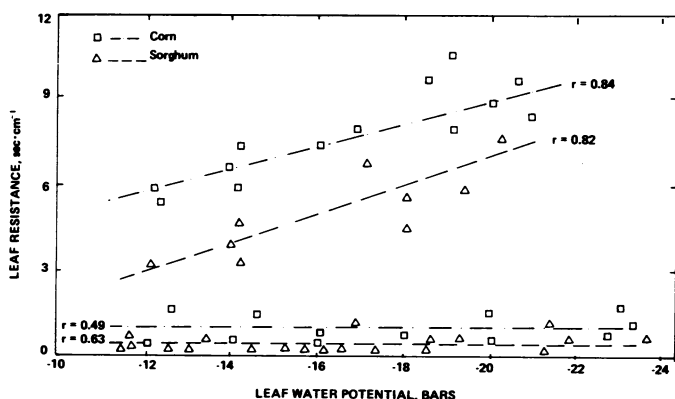

Fig. 1. Relationship between leaf water potential and leaf diffusive resistance of corn and sorghum. Upper lines represent relationship during vegetative growth and lower lines represent relationship during reproductive growth. Data from limiting and nonlimiting soil water conditions were pooled to derive relationships.

corn and sorghum. However, stomata appear to remain partially open as stress develops since resistance values of 30 sec cm^{-1} were obtained in the dark. Stomata of corn and sorghum do not respond to decreasing leaf water potentials after reproductive growth has been initiated, at least within the range of leaf water potentials observed in this study (Fig. 1). Resistances as low as 0.25 sec cm^{-1} were observed in both sorghum and corn during reproductive growth. Frank et al. (9) observed that the threshold value of leaf water potential required to induce stomatal closure in wheat became progressively less as the plant developed. Stomata of sorghum and cotton became less sensitive to water stress with increasing leaf age or if plants had been preconditioned by temporal water deficits (18, 23). Decreased leaf resistances with increased leaf age have also been reported for Xanthium strumarium L. (19). The relationship between leaf resistance and leaf water potential in cotton is not reported here, since we have previously observed that leaf resistances are very low throughout the season and the stomata are relatively insensitive to leaf water status (1).

Since leaf resistances were low during the course of reproductive growth, even slight regulation of water loss would prove beneficial. In this regard, the stomata of corn, sorghum, and cotton respond to changes in the humidity gradients between the leaf and air (Fig. 2). The response of cotton and sorghum is analogous to that observed for sunflower by Camacho-B et al. (7), whereas the response exhibited by corn was similar to their observation on sesame. Thus, the stomata of corn, sorghum, and cotton appear to respond to changes in the vapor pressure gradient in a manner similar to various other species (7, 10-12, 16, 17, 21). Although leaf resistances do not change greatly in response to increasing humidity deficits, the changes appear to be of sufficient magnitude to be beneficial in reducing water loss, albeit minimal.

Corn generally had lower transpiration rates at high humidity deficits than did cotton or sorghum (Fig. 3). The adaptive significance of stomatal response to humidity for plants adapted to arid and semiarid environments has been previously emphasized (10, 12, 17, 21). In the case of sorghum and corn, this response may be particularly important in view of the changes in stomatal response to bulk leaf water status during vegetative and reproductive growth. In the case of cotton, where stomata are relatively insensitive to leaf water status throughout the growing season (1, and unpublished observations in this laboratory), stomatal response to humidity would be an important mechanism for maximizing water use efficiency.

The influence of transpiration on leaf water potential was distinctly different in each of the species examined (Fig. 4). The initial decline in leaf water potential of sorghum (Fig. 4A) with increasing transpirational flux was similar to that observed by Camacho-B et al. (7) for woody species under laboratory conditions. Under nonlimiting soil water conditions, sorghum leaf water potentials approach steady-state values of approximately −15 bars, even as transpiration increases. This reponse is analogous to observations by Camacho-B et al. (7) indicating constant leaf water potentials in herbaceous species in response to increasing transpirational flux. Under limiting soil water conditions, sorghum leaf water potentials continue to decline in a linear manner as transpiration increases. The response of leaf water potentials at low transpirational flux was similar under limiting and nonlimiting soil water conditions. Extrapolation of the data to zero water flux would reflect a slightly curvilinear response with respect to both limiting and nonlimiting conditions, since we have previously observed that sorghum leaf water potentials increase to −1 to −3 bars on a diurnal basis (2). Under nonlimiting soil water conditions, sorghum exhibits an efficient water transport system capable of maintaining leaf water potentials at −15 bars. This suggests a variable internal resistance to water flux since absorption must equal transpira-

tional losses in order for a constant water potential to be sustained. As soil water availability decreases, changes in internal resistances cannot compensate for decreased absorption of water. Boyer (5) has thoroughly discussed the nature of these resistances.

Leaf water potentials of corn declined linearly in response to increasing transpiration (Fig. 4B). However, no differences could be ascertained between limiting and nonlimiting soil water conditions. In contrast to sorghum, corn leaf water potentials continue to decrease under conditions of high evaporative demand even if soil water is readily available. Internal resistances to water flow apparently do not change in corn, reflecting a less efficient water transport system. Subsequently, even when soil water is not limiting, leaf water potentials of corn would decrease to water stress levels rapidly if high evaporative demand conditions prevailed, perhaps the result of relatively high root resistance.

Cotton leaf water potentials decreased in response to increasing transpiration (Fig. 4C). Under both limiting and nonlimiting soil water conditions, leaf water potentials appeared to remain constant at high transpirational fluxes. Barrs (3) reported decreases in leaf water potential with increasing transpiration in
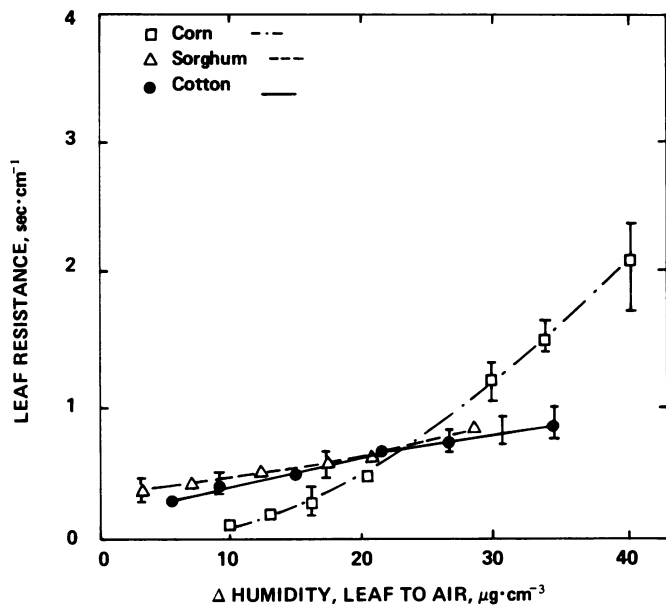

FIG. 2. Leaf diffusive resistance as a function of the absolute humidity difference between the leaf and air. Data were obtained from both irrigation treatments and after initiation of reproductive growth.
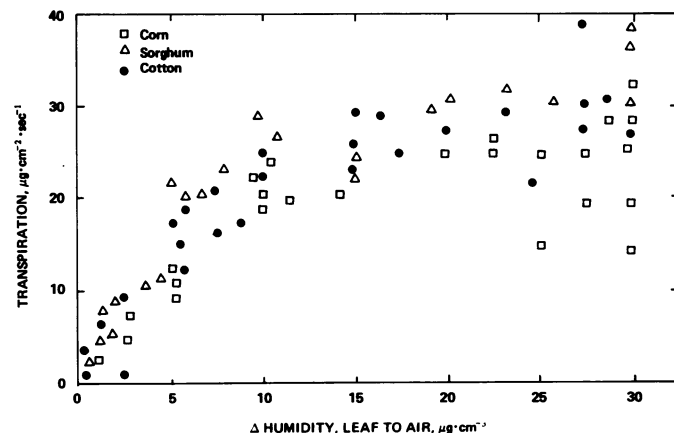

FIG. 3. Transpirational flux as a function of the absolute humidity difference between the leaf and air. Data were obtained from both irrigation treatments and after initiation of reproductive growth.
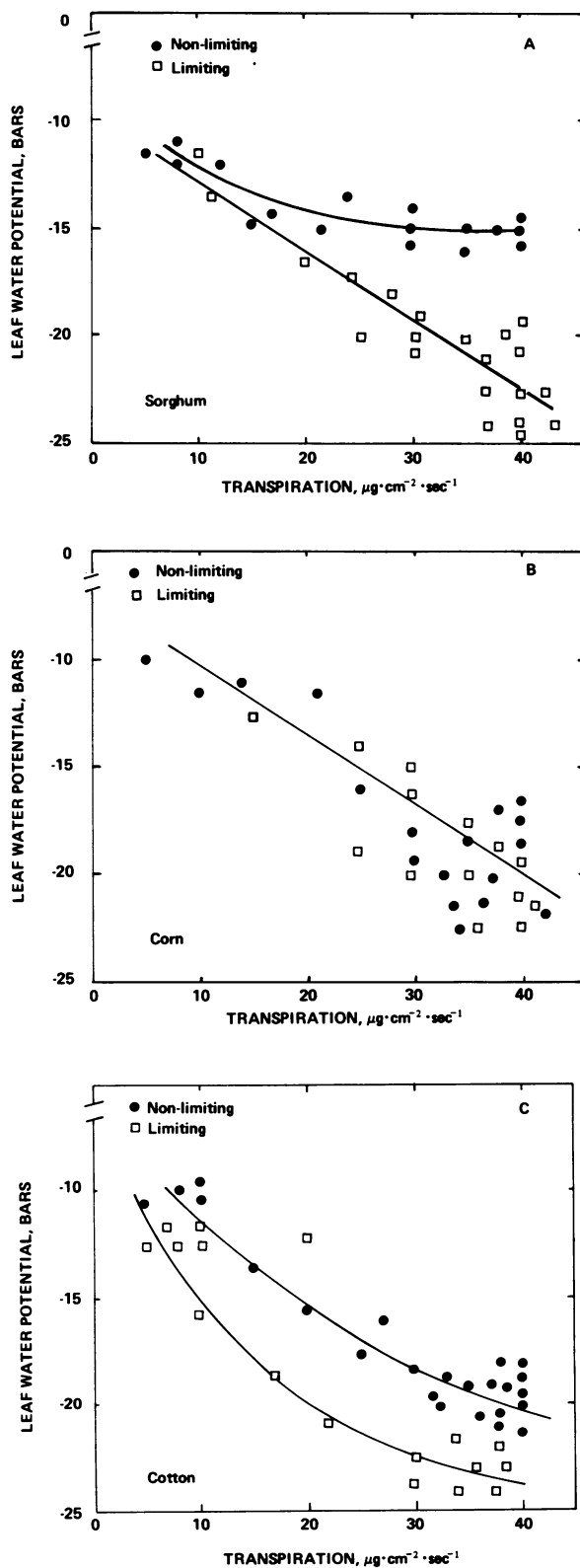

FIG. 4. Relationship between leaf water potential and transpirational flux under limiting and nonlimiting soil water conditions in sorghum (A), corn (B), and cotton (C). Data represent observed responses after initiation of reproductive growth.

Gossypium barbadense. However, Stoker and Weatherley (22) observed that leaf water potentials remained constant in cotton as transpiration increased, after initially decreasing from an approximate value of −6 bars at zero flux. The present data are

in partial agreement with both of these previous reports, since leaf water potentials of cotton initially declined and then seemed to approach a constant value at high flux. Extrapolation of both limiting and nonlimiting soil water curves indicate an approximate leaf water potential of −6 bars at zero flux, corresponding to observations by Stoker and Weatherley (22) and our previous observations indicating a maximum leaf water potential of −3 to −4 bars on a diurnal basis (2). At low transpirational flux, leaf water potentials are similar under both soil water conditions. However, the response curves diverge more rapidly as compared with sorghum. Moderate flux rates (10-20 $\mu g \cdot cm^{-2} \cdot sec^{-1}$) result in lower leaf water potentials in cotton than are observed in sorghum. This may reflect a less efficient water transport system or less variable internal resistance to water flow in cotton than in sorghum. Under nonlimiting soil water conditions, woody species characteristically appear to be less efficient in transporting water (8). However, under limiting soil water conditions, cotton leaf water potentials seem to decrease much more slowly at high transpirational flux (20-40 $\mu g \cdot cm^{-2} \cdot sec^{-1}$), whereas sorghum leaf water potentials continue to decline in a linear fashion. Thus, at greater water flux and limiting soil water conditions, cotton may be more efficient than sorghum in transporting water. The reverse situation would apply at high flux and nonlimiting soil water conditions.

Transpiration continued in all three species even as leaf water potential declined, suggesting that a threshold value of leaf water potential necessary to induce stomatal closure was not achieved. In this regard, under limiting soil water conditions, the plants were still capable of extracting water, perhaps the result of extensive root penetration or sufficiently high root capacitance that allows for water flux into the root. The relationship between relative water content and leaf water potential is distinctly different in each of the species (2, 20), suggesting that differences in water storage capacity might partially explain the leaf water potential-transpirational flux relationships.

Species differences in stomatal and nonstomatal regulation of water use are important with respect to drought adaptation (8). These experiments suggest that stomatal response to bulk leaf water status changes during ontogeny of the plant and that stomatal response to humidity may be particularly important in this respect. Efficient transport systems may confer drought tolerance to species when stomatal control of water loss is virtually nonexistent. Sorghum and cotton appear to be better adapted than corn to arid and semiarid conditions in this respect. Changes in the efficiency of the water transport system in response to soil water conditions are also important with respect to drought adaptation. Differences in sorghum and cotton with respect to water transport under limiting and nonlimiting conditions exemplify changes in this efficiency.

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